



# Species coexistence, intransitivity, and topological variation in competitive tournaments

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## ABSTRACT

Competitive intransitivity occurs when species' competitive abilities cannot be listed in a strict hierarchy, but rather form competitive loops, as in the game 'Rock–Paper–Scissors'. Indices are useful for summarizing intransitivity in communities; however, as with most indices, a great deal of information is compressed into single number. So while recent ecological theory, experiments, and natural history observations demonstrate that competitive intransitivity can promote species coexistence, the consequence of variation in the 'topology' of competitive interactions that is not accounted for by intransitivity indices is much less well understood. We use a continuous analytical model and two complementary discrete lattice models (one spatially explicit, the other aspatial) to demonstrate that such variation does indeed greatly affect species coexistence. Specifically, we show that although intransitivity indices are good at capturing broad patterns of coexistence, communities with different levels of intransitivity can have equal coexistence, and communities with equal intransitivity can have different coexistence, due to underlying variation in competitive network topology.

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## 1. Introduction

Intransitive competition can be described most easily using the simple analogy of the 'Rock–Paper–Scissors' game in which three strategies compete and each strategy is dominant to just one other: Rock smashes Scissors, Scissors cuts Paper, and Paper covers Rock. This is in contrast to hierarchical or completely transitive competition, which occurs if Scissors cuts Paper, but contrary to the game's tradition, yet perhaps more realistically, Rock smashes both Scissors and Paper. Numerous theoretical models have demonstrated that transitive competition quickly leads to a monoculture of the best competitor (e.g., Rock in the above transitive competition example), while intransitive competition contributes to greater coexistence (Czárán et al., 2002; Durrett and Levin, 1994, 1998; Gilpin, 1975; Huisman et al., 2001; Huisman and Weissing, 1999, 2001a, b; Kerr et al., 2002; Laird and Schamp, 2006, 2008; May and Leonard, 1975; Reichenbach et al., 2007; Szabó et al., 2004; Tainaka, 1988). Thus, intransitivity is a potential mechanism by which competition itself can promote coexistence—in contrast to most coexistence theories which require that competition be mitigated (Chesson, 2000; Huston, 1994; Tokeshi, 1999).

Furthermore, intransitivity has been identified for a wide variety of taxonomic groups, including plants (e.g., Lankau and Strauss, 2007; Shipley, 1993; Taylor and Aarssen, 1990), sessile marine organisms such as bryozoans, ascidians, cnidarians, sponges, and coralline algae (Buss, 1980, 1990; Buss and Jackson, 1979; Jackson, 1983), bacteria (Kerr et al., 2002), and mating strategies in lizards (Sinervo and Lively, 1996; Sinervo et al., 2007). Therefore, intransitive competition may be an important biological mechanism promoting genetic, species, and behavioral diversity in natural systems.

Competition is simplified in three-species models because only completely intransitive or completely transitive competition is possible (e.g., Durrett and Levin, 1994, 1998; Gilpin, 1975; Kerr et al., 2002; May and Leonard, 1975). However, competitive interrelationships can be increasingly complex as more species are considered (e.g., Huisman et al., 2001; Huisman and Weissing, 1999, 2001a, b; Karlson and Jackson, 1981; Laird and Schamp, 2006, 2008). For example, increasing the number of competing species also increases the number of different levels of intransitivity that are possible in a community of competitors (e.g., Laird and Schamp, 2008; Petraitis, 1979). This is true because an intransitive loop requires at least three species (as in Rock–Paper–Scissors), and with more than three species, it is possible to have multiple intransitive loops. Hence, indices of intransitivity (e.g., Bezembinder, 1981; Kendall and Babington Smith, 1940; Laird and Schamp, 2006, 2008; Petraitis, 1979; Slater, 1961), become increasingly continuous as the number of species increases. Moreover, theoretical models have revealed that these

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indices are powerful predictors of species coexistence (Laird and Schamp, 2006, 2008).

One drawback of intransitivity indices, however, is that they abstract a great deal of information regarding competitive relationships among community members (i.e., ‘competitive topologies’) into a single number. This is because the number of possible competitive topologies increases at a much faster rate than the number of species, and hence the number of possible levels of intransitivity (Electronic Supplementary Material 1). Topological variation that is not fully accounted for by intransitivity indices can be visualized by noting that assemblages with equal intransitivity can have different topologies (Fig. 1). Importantly, topological variation that is not accounted for by indices of intransitivity can impact coexistence (e.g., see the discussion of ‘pathway number’ in Laird and Schamp, 2006). In this paper, we use a continuous mean-field model as well as discrete spatial and aspatial lattice models, to demonstrate that although intransitivity indices are good predictors of broad patterns of coexistence, unexplored variation in competition matrix topology influences coexistence for five competing species.

## 2. Methods

### 2.1. Tournament matrices

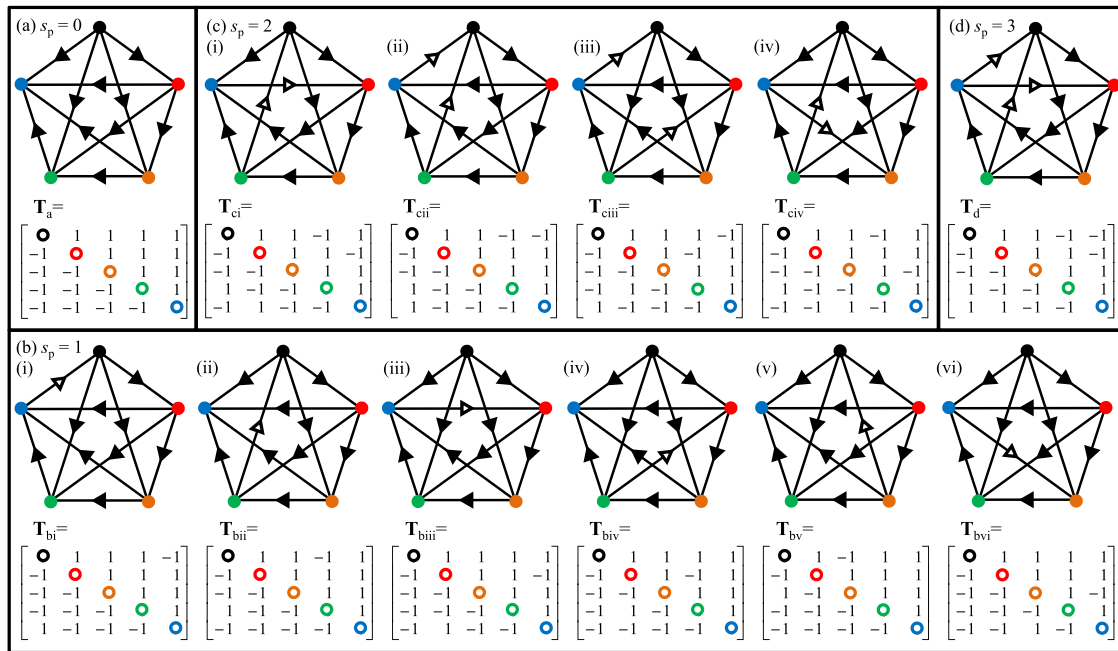
‘Tournament matrices’ describe the competitive relationships for all pairs of species in a community. They are similar to the ‘competitive outcomes matrices’ discussed in Laird and Schamp

(2006, 2008). A tournament matrix for  $s$  species has dimensions of  $s$  rows by  $s$  columns. If the species denoted by row  $i$  outcompetes the species denoted by column  $j$ , position  $(i, j)$  is filled with a ‘1’. Conversely, if the species denoted by row  $i$  is outcompeted by the species denoted by column  $j$ , position  $(i, j)$  is filled with a ‘-1’. If  $i = j$ , position  $(i, j)$  is filled with a ‘0’.

The number of possible tournament matrices increases explosively with the number of species. However, many of these are topologically equivalent (i.e., they are identical unlabeled graphs in the context of graph theory). For instance, the following two matrices are equivalent representations of Rock–Paper–Scissors (‘R–P–S’) competition:

$$\begin{matrix} 0 & -1 & 1 & 0 & 1 & -1 \\ 1 & 0 & -1 & -1 & 0 & 1 \\ -1 & 1 & 0 & 1 & -1 & 0 \end{matrix}$$

The left-hand matrix’s rows and columns can be ordered R–P–S, P–S–R, or S–R–P, whereas the right-hand matrix’s rows and columns can be ordered R–S–P, S–P–R, or P–R–S. The matrices are equivalent because one can be converted to another by a simple re-ordering of the rows and columns. Notwithstanding the redundancy of tournament matrices, there are still a huge number of unique tournament matrices as  $s$  becomes large (Goldberg and Moon, 1970). For example, while there are only two unique three-species tournaments (e.g., the traditional and modified Rock–Paper–Scissors games described in Section 1), there are 456 seven-species tournament matrices, and close to a million-billion-trillion 17-species tournament matrices (Electronic Supplementary Material 1).



**Fig. 1.** The twelve unique interaction web diagrams and tournament matrices for five-species communities. Panel names correspond with the ‘tournament names’ in Table 1, the example mean-field predictions in Fig. 2, and the  $x$ -axes of Fig. 3. Species are shown as nodes (circles) and their pair-wise competitive relations are shown as edges (arrows). Arrows point from competitive dominant to subordinate (e.g.,  $\bullet \rightarrow \circ$  means that the species denoted by the black node outcompetes the species denoted by the white node). An example tournament matrix is given for each interaction web: a ‘1’ means the row species outcompetes the column species, a ‘-1’ means the column species outcompetes the row species, and a colour ‘0’ is given when row = column (the 0s also provide the row and column corresponding to the node of the same colour; furthermore, their colours match up with the species in Fig. 2). (a) The ‘hierarchical’ case (Petraitis’  $t = 1$ , minimum number of reversals to convert the matrix to a hierarchy  $s_p = 0$ ; Petraitis, 1979). (b) The six unique manifestations of the ‘moderately intransitive’ case ( $t = \frac{2}{3}$ ,  $s_p = 1$ ). White arrowheads denote the competitive relations that would have to be reversed to convert these networks into the hierarchy given in (a) (for (bi)–(biii), the hierarchy in (a) is the only hierarchy within a single reversal; for (biv)–(bvi), there are two other hierarchies that are equally close—not shown). (c) The four unique manifestations of the ‘strongly intransitive’ case ( $t = \frac{1}{2}$ ,  $s_p = 2$ ). White arrow heads are the same as in (b) (for (ci), the hierarchy in (a) is the only hierarchy within a single reversal; for (cii), (ciii), and (civ), there are, respectively, one, two, and four other equally close hierarchies—not shown). (d) The ‘perfectly intransitive’ case ( $t = 0$ ,  $s_p = 3$ ). White arrowheads are the same as in (b) and (c) (there are four other equally close hierarchies—not shown). All other five-species tournament matrices are reconfigurations of the twelve shown here. Note that Petraitis’  $t$  is equal to one minus the minimum number of reversals needed to convert a tournament to a hierarchy ( $s_p$ ), divided by the maximum possible value of  $s_p$  for communities of a given size (for five-species communities,  $\text{MAX}(s_p) = M = 3$ ; see Table 1).

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